

COMPETITIVE EFFECTS OF INCREASED PLANT SPECIES RICHNESS AND INCREASED ENDEMIC
VERSUS NATIVE GENERALIST SPECIES DOMINANCE ON THE INVASIVE GRASS *MICROSTEGIUM*
VIMINEUM DURING OAK WOODLAND RESTORATION

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ABSTRACT

The hypothesis that species-rich assemblages are resistant to invasion by non-native species has generated considerable research and controversy. However, the relevance of such research to the conservation of biodiversity is questionable, given that local species richness often does not correlate with regional or global species richness, two metrics undoubtedly important to conservation. Furthermore, species of greater conservation interest (i.e. endemics) and widespread generalist species may compete differentially with non-native invasive species. To test whether plant species richness or species fidelity to a regionally rare habitat were more important in competitively suppressing an invasive species, I established a field competition experiment in an oak woodland in north-central Mississippi (USA) between the non-native invasive grass *Microstegium vimineum* and six native plant species of varying fidelity to fire-maintained open woodlands. Using a split-plot design, dense, established patches of *Microstegium* were treated with one of the three following native planting treatments or control: (1) a six species polyculture, (2) a monoculture of six individuals of a single species, or (3) a control simulating the soil disturbance of the plantings. I then monitored *Microstegium* percent cover through the 2015 growing season and into the spring of the following year. Emergence of the native species in the spring of 2015 was high (85% survival), which in turn appeared to initially suppress *Microstegium* seedling cover. This initial suppression of *Microstegium* was variable, with the native generalist species outperforming natives that are more highly indicative of open woodlands (i.e. endemics). However,

subsequent survival of all native species through 2015 was relatively low (38%), and there was no evidence of suppression of *Microstegium* either in the fall of 2015 or in the spring of 2016. Overall, these results indicate that of the six native species utilized here, the generalist species more indicative of disturbed habitats, yet also of less value to conservation, were more successful at reducing the emergence of this highly invasive grass. However, results also suggest that such a highly competitive invader may ultimately establish and proliferate, regardless of any initial resistance from resident species, possibly to the detriment of regional and global biodiversity.

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INTRODUCTION

As proposed by Elton (1958), the hypothesis that species-rich assemblages are resistant to invasion by non-native species has generated considerable research and controversy (Robinson et al 1995, Wiser *et al* 1998, Levine and D'Antonio 1999, Levine 2000, Zavaleta and Hulvey 2004, Stachowicz and Tilman 2005, MacDougall *et al* 2009). Diversity-mediated invasion resistance is largely influenced by classic niche theory, which predicts species-rich communities as having relatively high levels of niche saturation, thereby causing a reduction in potential colonization by non-resident species (Elton 1958; Stachowicz and Tilman 2005; MacDougall *et al* 2009). To this end, both experimental and theoretical studies have shown that diverse communities tend towards having reduced invasibility (Case 1990; Levine 2000; Zavaleta and Hulvey 2004). In contrast, some observational studies have shown positive relationships between native species richness and non-native species richness or abundance (Robinson *et al* 1995, Levine and D'Antonio 1999, Stohlgren *et al* 2001, Houlahan and Finlay 2004, Stachowicz and Tilman 2005), whereas other observational studies have shown that some negative relationships between native and non-native species can be explained by environmental factors that have opposite effects on native and non-native species (MacDougall and Turkington 2005, Surrrette and Brewer 2008, Brewer 2010). The apparent disparity between the results of experiments and theory on the one hand and the results of observational studies on the other has been reconciled by acknowledging and demonstrating that competition and numerous other factors (e.g., propagule supply, disturbance, resource supply) influence relationships between native and non-native species under natural conditions (Levine 2000, Davis et al. 2000, Stachowicz and Tilman 2005, Brewer 2011b). Regardless of whether factors other than

competition play a dominant role in influencing invasibility, if competition plays some role, reductions in species diversity could make communities more invulnerable (Levine 2000; Zavaleta and Hulvey 2004, Brewer 2010). For this reason, some ecologists have argued that, in addition to preserving other ecosystem functions, the prevention of species losses also reduces invasibility, thereby conveying a pragmatic reason for conserving biodiversity (Zavaleta and Hulvey 2004, Tilman *et al* 2014). Consequently, studies of diversity-invasibility relationships have the potential to inform conservation and land management practices, in addition to community assembly processes.

The notion that preservation of local species diversity in intact natural communities accomplishes two goals, preservation of global biodiversity and resistance to invasion, is based on the assumption that declines in global biodiversity are caused by worldwide declines in local species diversity within intact communities. This assumption has been challenged (Whittaker 1972; Alvarson *et al.* 1994; Brewer 2010; Vellend *et al.* 2013; Thomas 2013). Preserving local species diversity simply requires gains of species that equal or exceed local extirpations of species. In contrast, preserving global biodiversity requires land use and management practices that will ensure that global extinctions do not exceed the rate of speciation (Noss *et al.* 1995, Sax and Gaines 2003). Increases in local species diversity that result from higher colonization rates relative to local extirpation rates do not increase global biodiversity. Only speciation increases global biodiversity. In addition, local extirpation of widespread species is likely to have relatively little effect on global biodiversity compared to local extirpation of globally rare species. Habitat destruction is the main cause of extinctions and thus declines in global biodiversity, and losses of species-rich habitat to agricultural lands and residential development

undoubtedly also cause a reduction in local species diversity (Thomas 2013). Nevertheless, the more important effect of habitat destruction on global biodiversity may be through the destruction of rare habitats that support globally rare endemic species (Farnsworth 2007, Pimm *et al.* 2014) than through reduction in local species diversity, *per se* (Thomas 2013). Although more subtle habitat changes may significantly affect local species diversity without destroying an entire habitat, a recent meta-analysis of studies examining changes in local species richness revealed no net decline in local species diversity worldwide (Vellend *et al.* 2013). Declines in local species diversity in some communities were balanced by increases in local species diversity in others (Vellend *et al.* 2013). Whether the relatively few observed declines in local species diversity in some intact natural communities significantly contribute to global declines in biodiversity remains unclear. Therefore, while subtle habitat management that minimizes local extirpations of species within intact ecosystems may prevent some biological invasions (Levine 2000), it remains unclear whether such management practices are important for maintaining global biodiversity. Assessing how endemic species of globally rare habitats compete with invasive species may be of greater value to conservation of biodiversity and resistance to invasion.

Precisely how endemic species might differ from generalist native species in their competitive interactions with non-native invasive species is not entirely clear. When endemic species are also habitat specialists, one might expect them to be strong competitors, whereas generalists might more likely be fugitive species that must disperse away from competitors to persist (Platt and Weiss 1985; Nee and May 1992). To the extent that specialists associated with globally rare habitat are also good local competitors, management that increases their

abundance could have the dual benefit of preserving global biodiversity (by reducing local extinction of globally rare habitat specialists) and increasing community resistance to invasion. Such management need not increase local species diversity to be effective, however, because globally rare species need not be locally rare or sparse (Walker 1993). On the other hand, some widespread perennial plant species associated with productive, early and mid-successional habitats exhibit characteristics that confer high competitive ability, such as rapid vegetative growth rates and continued occupation of sites by virtue of their perennial life history [e.g., the Competitor strategy of Grime (1979)]. Management that favors such competitive generalists could reduce invasion, but by itself might not be particularly effective at preserving global (or local) diversity. Accomplishing both conservation objectives therefore might require management that simultaneously favors both habitat specialists and competitive generalists, assuming competitive displacement of specialists by generalists can be avoided.

In upland, oak-dominated forests of the eastern United States, the land management practices most likely to affect local species diversity and/or the abundance of habitat specialists are prescribed burning and canopy reduction associated with ecological restoration of fire (Hutchinson *et al.* 2005; Brawn 2006; Brewer *et al.* 2015). It is well understood that disturbance promotes increases in diversity and abundance of groundcover plants in oak-dominated systems (Hutchinson *et al.* 2005, Brawn 2006, Brewer *et al.* 2015, Brewer 2016). Considering fire as a low-intensity disturbance, positive post-fire responses of native herbaceous species are often caused by reduced competition from fire-sensitive species and increases of light at the soil level (Gilliam *et al.* 1988). Reductions in competition from fire-sensitive species and increases in resource availability, however, can also favor non-native species (Davis *et al.* 2000;

Huston 2004). Unfortunately, the reestablishment of natural fire regimes to historically fire-maintained ecosystems is a community-level disturbance that can promote increases of invasive plant species (Crawford *et al.* 2001, Glasgow and Matlack 2006, Keeley 2006, Brewer *et al.* 2015). Given greater management interest in using prescribed burning in eastern US upland forests (Abrams 1992, Matlack 2013), the undesirable consequence of directly increasing species invasion presents a management challenge for restoration practitioners. Considering this potential dilemma, it is perhaps necessary to determine factors biotic or otherwise that potentially limit the proliferation of invasive species already established at natural sites.

Although ecological restoration can reduce competition from fire-sensitive species, to the extent that it increases the abundance of multiple fire-tolerant species, such management has the potential to increase competition among fire-tolerant species that respond positively to such disturbances (Brewer 2011a). Such disturbance-mediated increases in competition associated with ecological restoration of fire provide an opportunity to examine the effectiveness of competitive suppression of non-native fire-tolerant species by established native fire-tolerant species. By comparing the competitive effects of endemic habitat specialists and widespread generalists that respond favorably to fire restoration on invasive species that likewise respond favorably to fire restoration, one could determine whether fire restoration and planting of selected native species could be used to simultaneously preserve biodiversity and reduce the proliferation of invasive species.

An invader of eastern US deciduous forest with increasing notoriety for positive responses to prescribed fire is the exotic *Microstegium vimineum* (Trin.) A. Camus. An annual C₄ grass native to East Asia, *Microstegium* was first discovered in Tennessee in 1919, most likely

arriving by seed from packaging material (Fairbrothers and Gray 1972). Since its introduction, the exotic grass has spread to twenty-four US states, with its current distribution ranging from Texas to Massachusetts (USDA 2016). In the initial stages of establishment, *Microstegium* appears to favor disturbed habitat such as roadsides and forest edges (Cole and Weltzin 2004; Christen and Matlack 2009). Both floodwaters and human activity along roadways facilitate the local dispersal of *Microstegium*, as well as its long-distance dispersal along road axes (Christen and Matlack 2009; Tekiela and Barney 2013). However, little is known about long-distance dispersal that allows for patch founding in the interior of forests, with only anecdotal evidence supporting its spread by animals (Mehrhoff 2000; Warren *et al* 2011). Following its establishment, *Microstegium* can alter forest succession dynamics, competitively suppress native plant species and increase the intensity of prescribed fires (Flory and Clay 2010; Brewer 2011b; Emery *et al.* 2011; Wagner and Fraterrigo 2015; Brewer *et al.* 2015). In addition, the invasive grass produces a prolific seed bank, potentially allowing sub-populations to persist through time in the forest understory (Gibson *et al.* 2002).

In this study, I utilized an ongoing oak-hickory woodland restoration experiment in north-central Mississippi (USA) to test several hypotheses regarding competition between the non-native invasive grass *Microstegium vimineum* and native plant species of varying fidelity to open woodlands. Specifically, I tested the following hypotheses: (1) species-rich (i.e. polyculture) and single-species (i.e. monoculture) planting treatments of native plants indicative of a variety of open habitats will suppress the emergence and growth of the *Microstegium* (hereafter, the general suppression hypothesis); (2) overall, polyculture treatments will suppress the emergence and growth of *Microstegium* more so than

monoculture treatments (hereafter, the diversity-mediated suppression hypothesis); and (3) the greater competitive suppression of *Microstegium* of the polyculture treatments will result from the presence of a few relatively highly competitive species (hereafter, the selective suppression hypothesis).

METHODS

Study Site

The study described here took place in upland mesic hardwood forest at Strawberry Plains Audubon Center, an ~1000-ha wildlife sanctuary located in the loess plains of north-central Mississippi, that is currently undergoing oak-hickory woodland restoration. In 2004 approximately 1 hectare treatment and control areas were established in a paired design at two sites within Strawberry Plains separated by approximately 2 km [site 1 (34°49'60"N, 89°28'32"W); site 2 (34°49'52"N, 89°27'7"W)]. Beginning in 2004 at site 1 and in 2008 at site 2, individuals of tree species historically absent from the mesic uplands of north-central Mississippi [e.g. *Liquidambar styraciflua* (sweetgum), *Nyssa sylvatica* (blackgum), *Prunus serotina* (black cherry)] were thinned from 30 x 30 m plots within the treatment area (see Brewer 2001 and Surrlette et al. 2008 for pre-settlement tree species composition). In addition, tree species known to be historically present but in lower abundances in these upland forests were thinned from the canopy [e.g. *Quercus falcata* (southern red oak), *Carya tomentosa* (mockernut hickory)]. From 2004 to 2014, site 1 was burned biennially, typically in March or April. Likewise, the treatment plot at site 2 was burned biennially from 2008 to 2012, every March or April. In 2014, coinciding with the restoration treatments at both sites, there were significant increases in native groundcover species indicative of fire-maintained open habitats relative to the control areas (Brewer *et al.* 2015). However, there were also significant increases in *Microstegium* in the treated plots at both sites (Brewer *et al.* 2015). Soils at both sites are generally a mix of Providence silt loam and Cahaba sandy loam, with Providence silt

loam slightly more prevalent at site 1 and Cahaba sandy loam slightly more prevalent at site 2 (Morris 1981, Maynard and Brewer 2013).

Experimental Design

In November 2014, using a split-plot design, within the treated areas, I established twelve ~3-m² whole plots within all the patches of *Microstegium* I could find that were large enough to spatially contain them (Fig. 1). I was able to establish a total of twelve whole plots at both sites combined. I established two whole plots at site 1 and ten whole plots at site 2 and made no attempt to account for site as a factor. The whole-plot treatment factor was the species group that comprised the monoculture split-plot treatment, with two levels (open woodland indicator and disturbance indicator). Each species group consisted of three species (described below). Species was considered a random factor nested within species group, and there were two replicate plots per species. Each whole plot consisted of three 0.75 m² subplots (for a total of 36 subplots), with each subplot containing one of three of the following split-plot treatments: (1) a polyculture of six species consisting of one individual per species; (2) a monoculture of six individuals of a single species; or (3) a control treatment simulating the soil disturbance of the planting treatments. Each of the six species comprising the monoculture subplot was assigned randomly to two of the twelve whole plots. I then randomly assigned one of three planting treatments (i.e. the split-plot treatment) at the subplot level. This design allowed me to statistically test whether differences in *Microstegium* emergence and establishment between polycultures and monocultures were due to a species richness effect versus a species identity effect.

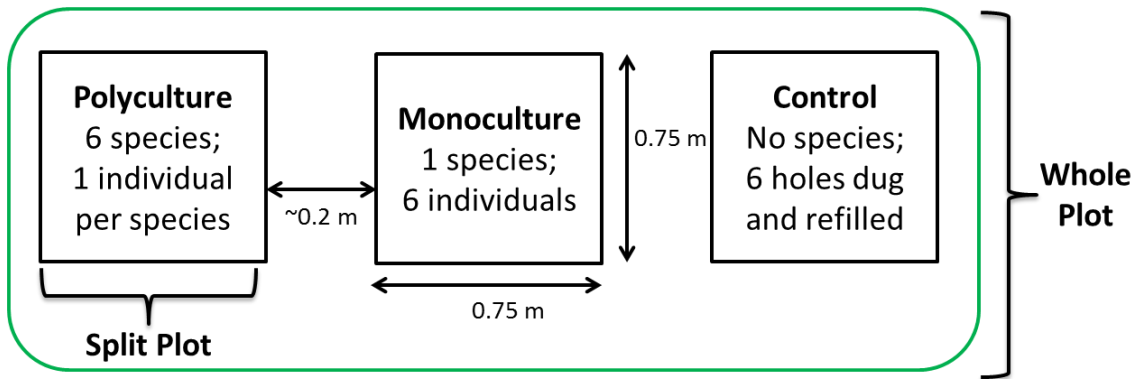


Figure 1 - Layout of the split-plot experimental design. Subplots were spaced apart by approximately 0.2 m to avoid edge effects. In total, 12 whole plots were established across sites 1 and 2. The identity of each whole plot was defined by the randomly assigned species identity of the Monoculture split-plot treatment.

For the polyculture and monoculture planting treatments, I chose the following six native perennial plant species: *Coreopsis tripteris* (tall coreopsis), *Desmodium laevigatum* (smooth tick trefoil), *Helianthus silphoides* (Ozark sunflower), *Saccharum giganteum* (sugarcane plumegrass), *Schizachyrium scoparium* (little bluestem), and *Solidago canadensis* (Canada goldenrod). I based my selection of these six species on several criteria. Firstly, I selected three species that were indicative of open habitats, including globally rare habitats such as fire-maintained open woodlands, savannas, and barrens, as well as three species relatively more indicative of globally common early- or mid-successional habitats such as old fields and roadsides. Habitat indication statuses were derived from Brewer and Menzel (2009), as based on the habitat associations of Jones (2005), and used to group the six species into one of two species groups (the whole plot treatment factor), either as those indicative of fire-maintained open woodlands (hereafter, woodland indicators), or those much more relatively indicative of disturbed early- and mid-successional habitats (hereafter, disturbance indicators). Secondly, the six species were drawn from a pool of native species responding positively to the

oak-hickory woodland restoration treatments at Strawberry Plains Audubon Center (Brewer and Menzel 2009; Brewer *et al.* 2015). Thirdly, the species chosen here varied widely in their geographic distribution and level of endemism, with several species ranging across the entire contiguous United States, southern Canada, and/or Mexico (*Schizachyrium*, *Solidago*), to one species being nearly restricted to the Mid-South United States (*Helianthus*). Lastly, I compiled an assemblage that would represent a variety of plant functional groups. Using species information derived from the USDA PLANTS Database (2016), I placed the six species here into one of the three following functional groups: C4 grass, C3 forb, and C3 nitrogen-fixing legume.

Establishment of Transplants

In December 2014, transplants of the native species were collected (144 plants total) on-site near site 1. Bulk soil was removed from the roots, all aboveground tissues were removed, and the plants were weighed and transplanted as cuttings. To minimize edge effects of the treatments, each subplot was spaced approximately 0.2 m from neighboring split-plots. The transplants were then individually marked with a metal wire and tag and received 150 mL of water to stabilize soil surrounding the plant roots. For polycultures, the locations of all six individual transplants were randomized within each plot. Control treatments were applied to simulate a comparable amount of soil disturbance associated with the planting treatments. Therefore, six holes corresponding to planting locations in treated plots were dug, refilled with soil, and then received approximately 150 mL of water.

Data Collection

To quantify the natural emergence and success of *Microstegium*, I measured *Microstegium* percent cover in a 20 x 20 cm sub-subplot centered on each individual transplant

or control treatment (six sub-subplots total per subplot), during mid-May 2015, early October 2015, and mid-May 2016. Respectively, these dates coincide with the approximate emergence and peak biomass of *Microstegium* at 34°49'N. I also followed the emergence and survival of the native transplants through the 2015 growing season, as well their subsequent emergence in spring 2016. All native species utilized in this study were long-lived warm-season perennials that undergo senescence of all or most aboveground tissues. Therefore, survival through the growing season was assessed by the presence of at least some aboveground green tissue (i.e. stem and/or leaves) through early- to mid-October and the following spring.

Measurements of the native transplants included the following: stem height and length of longest leaf for the forbs (*Coreopsis*, *Desmodium*, and *Helianthus*), and shoot number, height of tallest stem, and length of longest leaf for the grasses (*Saccharum*, *Schizachyrium*). Reproductive allocation for the transplants was quantified by the following: counts of the number of flowering culms per plant (*Schizachyrium*), length and width of flowering panicle per plant (*Saccharum*), and counts of capitula and/or seed pods (*Coreopsis*, *Helianthus*, *Desmodium*). To account for variation of light availability and spring leaf litter on the emergence, growth and survival of *Microstegium* and the native transplants, I measured canopy openness and percent leaf litter cover at each subplot and sub-subplot, respectively. Canopy openness for 2015 and 2016 were quantified by averaging four orthogonal readings from a spherical concave canopy densiometer.

Data Analysis

Separate split-plot analysis of variance (ANOVA) tests were used to compare differences of mean *Microstegium* cover between split-plot treatments (polyculture, monoculture, and

control) for 2015 and spring of 2016. The general suppression hypothesis would be supported by a significant split-plot effect, followed by a significant planned contrast of the monoculture and polyculture treatments vs the control, such that mean *Microstegium* cover was significantly higher in the control. Likewise, the diversity-mediated suppression hypothesis would be supported with a planned contrast of the monoculture vs polyculture treatments, such that mean *Microstegium* cover was significantly higher for the monoculture treatment. To address the selective suppression hypothesis, I first averaged *Microstegium* percent cover over the two replicates per species and then used the species x split-plot interaction nested within species group to test the species group x split-plot interaction. A significant species group x split-plot interaction result from the split-plot ANOVA would then indicate that the difference in *Microstegium* cover between polycultures and monocultures depended on whether the species comprising the monoculture was a woodland indicator or a disturbance indicator, supporting the selective suppression hypothesis.

If split-plot ANOVA revealed significant differences between treatments with respect to their effects on *Microstegium* cover, then additional, separate split-plot ANOVAs were run with alternative response variables (spring leaf litter cover, initial transplant weight, canopy openness), to address the possibility that such variables were accounting for the observed patterns in *Microstegium* cover. For example, if leaf litter was responsible for significantly lower emergence of *Microstegium* in experimentally treated subplots, then a split-plot ANOVA with leaf litter as the response variable would likely reveal significantly higher litter cover in those subplots. Prior to analysis, initial transplant weights and leaf litter cover values were averaged across the six species per subplot and six cover values per subplot, respectively.

Although the competitive effects of *Microstegium* on the native transplants could not specifically be examined in this study, I used logistic regression to analyze the main effects of *Microstegium* cover on the survival of native transplants through 2015 and emergence in 2016, thereby examining the relationship between *Microstegium* productivity and transplant survival. In addition to *Microstegium* cover, the main effects of canopy openness and habitat indication (woodland or disturbance) on transplant survival were tested. *Microstegium* cover, canopy openness, leaf litter cover, and initial weight of the native transplants were checked for normality and homoscedasticity and transformed as necessary. I used the Wald test to determine significance of the predictors for the logistic regression. ANOVA tests were conducted using JMP version 5 and the logistic regression analysis was done using R version 3.1.1.

RESULTS

Survival of the native transplants in the spring of 2015 was high, with over 85% of all transplants emerging, which in turn appeared to initially suppress *Microstegium* cover. Coinciding with high transplant emergence, *Microstegium* cover in spring 2015 was significantly different among the three split-plot treatments ($F_{2,8} = 17.73$, $p < 0.01$). In support of the general suppression hypothesis, an orthogonal contrast revealed highly significant differences between the two planting treatments combined and the control, with the polyculture and monoculture treatments having significantly lower *Microstegium* cover relative to the control ($t_8 = 5.78$, $p < 0.01$; Fig. 2). Although *Microstegium* cover, on average, was slightly lower in polycultures than in monocultures (33.79 vs. 36.53%, respectively, $MSE = 1.33\%$), the contrast of the effect of polycultures versus that of monocultures on *Microstegium* cover was not statistically significant ($F_{1,8} = 2.12$, $p = 0.18$). Hence, I found no support for the diversity-mediated suppression hypothesis in this study (Fig. 2). However, the split-plot treatment by species group interaction approached significance ($F_{2,8} = 4.41$, $p = 0.05$), warranting an examination of the interaction components. In support of the selective suppression hypothesis, the difference in *Microstegium* cover between polycultures and monocultures depended on whether the monoculture species was a disturbance indicator or a woodland indicator (Fig. 2). Specifically, the cover of *Microstegium* appeared to be reduced in polycultures compared to monocultures of woodland indicators but not compared to monocultures of disturbance indicators (Interaction contrast $F_{1,8} = 8.76$, $p = 0.02$; Fig. 2).

Table 1. Summary of split-plot ANOVA and orthogonal contrasts for spring 2015

Microstegium cover. Whole plot effect is Species group (Sg); split-plot effects are the split-plot treatment (Sp; monoculture, polyculture, or control) and species group by split-plot interaction (Sg x Sp). Orthogonal contrast sources are monoculture (M), polyculture (P), control (C), woodland monoculture (WM), disturbance polyculture (DP), woodland polyculture (WP), and disturbance monoculture (DM).

Source	df	F	p
Species group (Sg)	1	0.17	0.69
Whole-Plot Error	4		
Split-plot treatment (Sp)	2	17.74	<0.01
Contrast: M, P vs. C	1	33.36	<0.01
Contrast: M vs. P	1	2.11	0.18
Sg x Sp	2	4.41	0.05
Contrast: WM,DP vs. WP,DM	1	8.76	0.02
Split-Plot Error	8		
Total	17		

The initial negative effects of plantings of these native perennials on *Microstegium* cover did not appear to be the result of potentially confounding artifacts. On average, spring 2015 leaf litter was marginally higher in polycultures, relative to monocultures and controls (35.25%, 32.33%, and 31.0%, respectively); however, a split-plot ANOVA run with log-transformed spring 2015 leaf litter cover as the response variable did not reveal significant differences of litter between split-plot treatments or a significant interaction ($p = 0.19$, $p = 0.55$; for main effects test and interaction components tests, respectively). Similarly, canopy

openness was higher on average in the planting treatments relative to the controls, with the monocultures, polycultures, and controls having 12.15%, 11.63%, and 9.9% canopy openness, respectively. Yet, a separate split-plot ANOVA run with spring 2015 canopy openness as the response variable did not indicate any significant differences between these treatments or a significance of the treatment by species group interaction ($p = 0.42, p = 0.51$). Finally, to examine initial cutting sizes between monocultures, I ran a nested ANOVA with the initial wet weight of the transplants as the response variable. On average, cuttings transplanted into woodland monocultures were actually larger than cuttings used in disturbance indicator monocultures (23.61 g vs. 21.19 g), yet the difference was not statistically significant ($p = 0.69$).

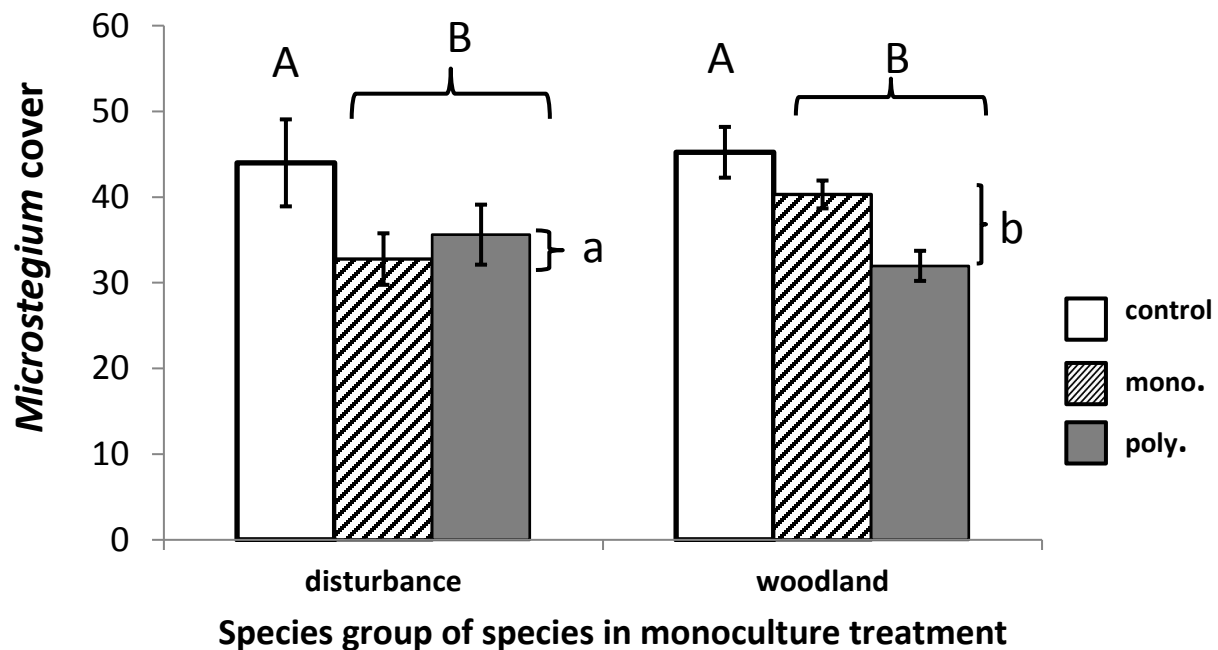


Figure 2 – *Microstegium* emergence in spring of 2015 for whole plots grouped into species groups (disturbance or woodland indicator in monoculture treatment). Capital letters denote significant split-plot effects, and lower case letters denote significant species group x split-plot treatment interaction. Values are mean *Microstegium* cover \pm 1 standard error.

In contrast to the high initial emergence and survival of the native transplants, survival (i.e., presence of aboveground green tissue) through 2015 was relatively low, with only 38% of all transplants persisting or remaining green until fall senescence and only 13% of all transplants flowering. Furthermore, split-plot ANOVA did not indicate any significant differences between the split-plot treatments or significance of the split-plot by species group interaction for *Microstegium* cover in the fall 2015 ($F_{2,8} = 0.67$, $p = 0.54$; $F_{2,8} = 0.803$, $p = 0.48$). For transplant survival through 2015, logistic regression revealed a significant main effect of canopy openness, with probability of survival significantly higher in subplots with greater light availability ($z = 3.129$, $p < 0.01$). In addition, the main effect of habitat indication was highly significant, with woodland indicators being much more likely to survive through 2015 relative to disturbance indicators ($z = 3.76$, $p < 0.01$; Fig. 3). Rather surprisingly, initial size of the native transplants and fall 2015 *Microstegium* cover were not significant in predicting survival ($z = -0.99$, $p = 0.32$; $z = -1.37$, $p = 0.17$). Contrasting sharply with spring 2015 emergence, there were also no significant differences of spring 2016 *Microstegium* cover between split-plot treatments and no significance of the species group by split-plot treatment interaction ($p = 0.22$; $p = 0.43$; Fig. 4).

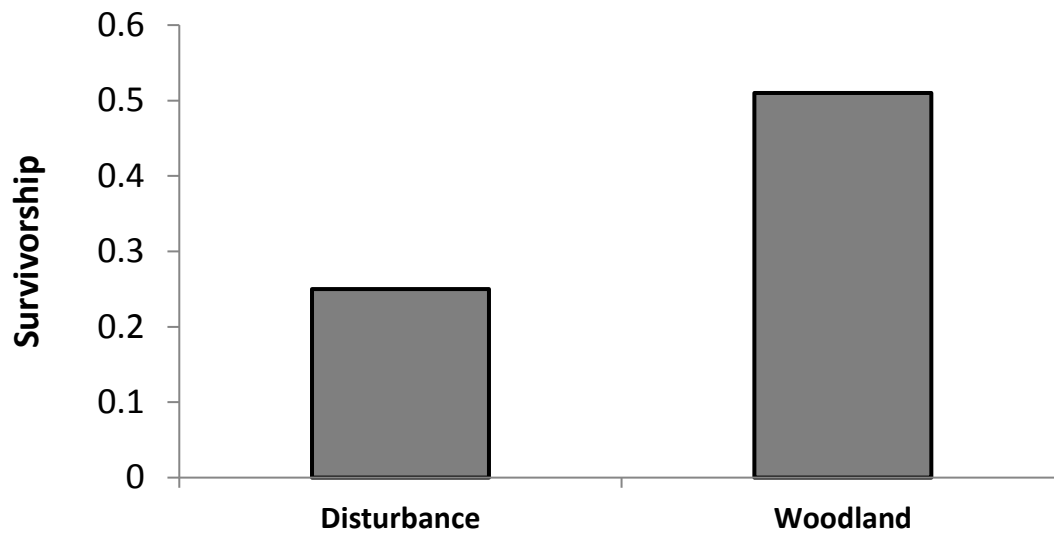


Figure 3 – Survivorship of native transplants through year 1 based on species group, either disturbance or woodland habitat indicator ($z = 3.759$, $p < 0.001$). Values are proportions of species for each species group that survived through year 1 to the total number of species transplanted per group (72 individuals).

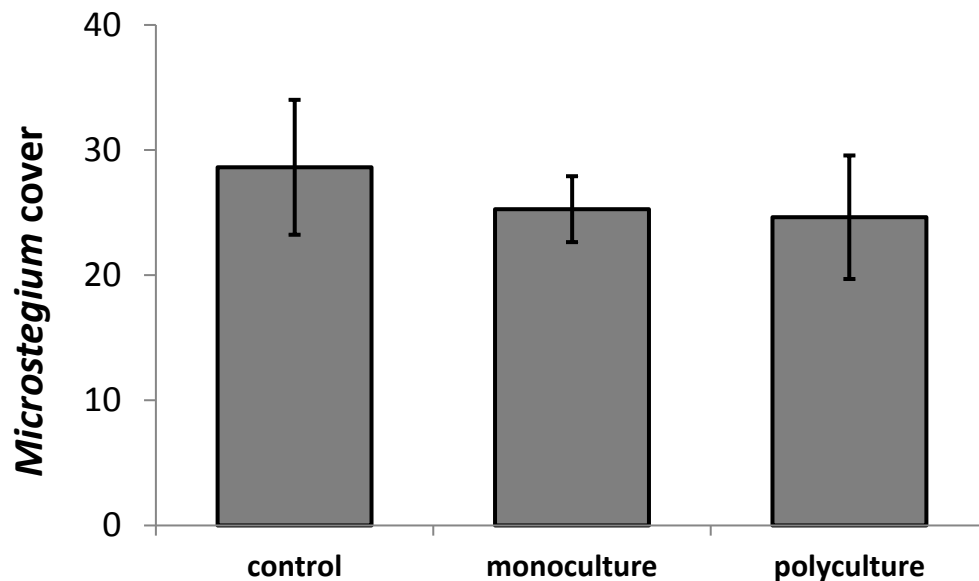


Figure 4 - *Microstegium* emergence in spring of year 2 (2016) grouped by split-plot treatments. Values are mean *Microstegium* cover and error bars are +/- 1 standard error.

DISCUSSION

The results of this study provide support for initial competitive effects of native plant species of varying fidelity to open woodlands on the non-native invasive grass, *Microstegium vimineum*. Specifically, my hypotheses of general competitive suppression and selective suppression of *Microstegium* were supported. Conversely, there was no support for my hypothesis of diversity-mediated suppression, in that polycultures of native plant species, on average, were no more effective in reducing *Microstegium* cover than were monocultures of native species. The initial competitive effects of plantings of native perennial plants that respond well to fire restoration on *Microstegium*, however, did not last beyond the first spring of the study. Neither the number nor the identity of planted species appeared to affect *Microstegium* cover in the second spring.

The initially negative effect of planting natives (irrespective of species number) on the emergence and establishment of a highly competitive non-native species is consistent with the hypothesis that even highly competitive non-native species may initially benefit from disturbances that reduce competition from native plants (Brewer 2010, 2011a). Such initial suppression may be short-lived, however, when dealing with highly competitive invaders (i.e., the species that are of greater conservation concern). Such a potential shift in competitive effects between resident species and invaders over time may help explain why many invaders known to have strong competitive effects on native species in relatively undisturbed systems also benefit (at least initially) from reduced competition caused by disturbances (Brewer and Bailey 2014).

The lack of support for the diversity-mediated suppression hypothesis in the current study contrasts with the results of studies employing more commonly used plant invasion experimental designs (i.e. simulated invasion of plant communities by non-native propagule addition; Levine 2000; Kennedy *et al.* 2002; Zavaleta and Hulvey 2004; Maron and Marler 2007). The reasons for these conflicting results are not entirely clear. One possibility is that the abundant propagule supply in the seed bank of firmly established patches of *Microstegium* (Gibson *et al.*), combined with the favorable abiotic conditions for the growth of *Microstegium* (spring fire and canopy openings), simply overwhelms any overyielding advantage that a diverse assemblage of residents might have over a competitively superior invader (Levine and D'Antonio 1999, Levine 2000, Brewer 2008, Corbin and D'Antonio 2010). Although in general, theoretical and experimental studies have provided support for diversity-mediated resistance to invasion, there is not agreement as to whether diverse assemblages can resist invasion by species that are vastly superior competitors to the residents (Case 1990, Levine and D'Antonio 1999). Future theoretical and experimental treatments of diversity-mediated invasion resistance need to focus more specifically on invaders with a large competitive advantage over resident species (e.g. Brewer 2008, Corbin and D'Antonio 2010). Given that these invaders likely represent the greatest threat to biodiversity, such theory and experiments will also be the most relevant to conservation of biodiversity.

Although I found no support for diversity-mediated suppression, there was evidence that polycultures were initially more effective at suppressing *Microstegium* than were monocultures of one of the species groups (woodland indicators), thus supporting the selective suppression hypothesis. The reason for the apparently greater initial competitive effects of the

disturbance indicators (*Saccharum*, *Schizachyrium*, *Solidago*) relative to the woodland indicators (*Coreopsis*, *Helianthus*, *Desmodium*) is not clear. One possibility is an initial size bias, where larger initial transplant sizes, particularly for *Saccharum* and *Solidago*, may have been responsible for the greater initial competitive effects. However, initial transplant weight did not differ significantly between the woodland and disturbance species groups. In addition, spring leaf litter cover and overhead canopy openness did not vary significantly between subplots that had different split-plot treatments, suggesting that these two important variables for seedling emergence were also not driving the differences in *Microstegium* cover.

The apparently higher initial competitive effects of the disturbance indicators, which included two C4 grasses, *Saccharum giganteum* and *Schizachyrium scoparium*, could in part be explained by their higher functional overlap with *Microstegium* relative to the woodland indicators, which exclusively represented the C3 forb and C3 nitrogen-fixing legume functional groups. Like *Saccharum giganteum* and *Schizachyrium scoparium*, *Microstegium* utilizes the C4 photosynthetic pathway. Such relationships of high functional overlap and/or functional equivalence between an invader and one or a few resident species have been used recently to explain increased invasion resistance of experimentally manipulated plant communities (Hooper and Dukes 2010, Byun 2013). *Saccharum* and *Schizachyrium* are perennial bunchgrasses, however, a life cycle and growth form quite dissimilar from the annual cycle and creeping, decumbent habit of *Microstegium*. Finally, it is possible that the variation in initial *Microstegium* cover could be explained by some unaccounted for variable(s) (e.g. plant-soil feedbacks, presence or absence of mycorrhizal association). Regardless, the initial treatment

effects were countered sharply an absence of competitive effects on *Microstegium* in the fall of year 1 and spring of year 2, as well as high transplant mortality.

Out of the six native plant species utilized here, those with the highest initial competitive effects were also those with considerably wider geographic ranges and with a relatively higher affinity for disturbed early- and mid-successional habitats. Although promising strictly in the sense of providing some suppression of an invader, usage of such common, widespread species in planting treatments for *Microstegium* would serve little benefit towards the preservation of global biodiversity. On the other hand, the woodland indicators did have a much greater probability of surviving to the end of year 1 relative to the disturbance indicators. Yet management to increase the abundance of these rarer, more range-restricted species, while valuable conservation-wise, would seemingly offer no initial competitive suppression of *Microstegium*. In general, there is evidence that some disturbance indicator species are responding positively to the oak woodland restoration treatments at the sites used in this study (Brewer *et al.* 2015), yet their higher observed mortality relative to the woodland indicators could largely be a consequence of their general shade intolerance. Some subplots within established *Microstegium* patches had less than 5% overhead canopy openness, values exceedingly low for moderately shade intolerant species such as the native C4 grasses used here. In contrast, *Microstegium* is known to possess relatively high shade tolerance for a C4 grass (Winter *et al.* 1982), having even been observed setting seed in deep shade within some mesic forests of the Eastern US (Cheplick and Fox 2011).

The reasons for the high mortality of the native transplants later in the growing season of 2015 are unclear, but an obvious possibility is increasing competition from *Microstegium*

during the growing season. The competitive effects of *Microstegium* on transplant survival were not directly examined in this study. Nevertheless, I attempted to quantify them indirectly using logistic regression. Results relating transplant survival, however, to *Microstegium* cover provided no evidence of a lower probability of survival with increasing cover of the invasive grass. Logistic regression might not have provided an accurate assessment of the competitive effects of *Microstegium* on the transplants, however, for the following reasons. First, because the experimental plots were established within high-density patches of *Microstegium*, with the exception of a couple of outliers with 11 and 12% cover, most subplots may have contained enough *Microstegium* to have exhibited a negative effect on the transplants. Hence, if a minimum threshold of *Microstegium* cover necessary for negative effects was exceeded in most of the subplots, and if these negative effects plateaued at higher levels of cover, then logistic regression would likely not reveal a negative effect of cover on survival. Second, the higher mortality of *Saccharum* and *Schizachyrium* (grasses in the disturbance indicator group) while in the presence of *Microstegium* is consistent with a previous study suggesting stronger suppression of graminoids by *Microstegium* in a mesic hardwood forest (Flory 2009). Similar patterns were also found in a California grassland, where Case *et al* (2016) showed that annual grasses were more likely to be displaced by an invading non-native annual grass than were forbs. Such results do not necessarily conflict with the interpretation that higher functional overlap between *Microstegium* and the native grasses may explain greater competitive effects during the spring emergence of *Microstegium*. In essence, the native perennials in the current study were competing initially as large cuttings with relatively small *Microstegium* seedlings. However, low light availability throughout the growing season combined with the ability of

Microstegium to persist in such environmental conditions may have led to compounding effects of shade intolerance and interspecific competition, causing the higher mortality observed for the native grasses relative to the forbs. Third, and perhaps most important, results of an ongoing experiment using the same transplant species at the same sites revealed a highly significant and positive effect of *Microstegium* removal on transplant survival by the end of the first growing season (Brewer and Moyer, unpublished data). Clearly, *Microstegium* is a superior competitor to the native plant species studied here.

Overall, the results of this study suggest that a six species assemblage of large native plants with a range of habitat fidelity to open oak woodlands can be planted into established patches of the highly invasive non-native grass *Microstegium vimineum*, initially survive, and reduce its emergence. Nevertheless, the competitive effects of the natives appear to vary significantly between species and are ephemeral, not lasting through the first growing season of when the plantings occurred. The native species that are more indicative of a rare habitat type (open oak woodlands), while not having greater initial competitive effects, were better suited than the disturbance indicators to long-term survival within patches of the invasive grass, perhaps due to their greater tolerance of partially shady conditions in the oak woodland where this study took place. In contrast to predictions of theory and results of previous experimental studies, diverse plantings of native species were not more effective at reducing the initial emergence of *Microstegium* than monocultures. Results do suggest that habitat management to increase the abundance of the disturbance indicators (i.e. monoculture plantings and canopy thinning) could potentially improve the biotic resistance of this system to such highly invasive species as *Microstegium*, at least initially. However, such species may need

to be planted at higher densities than was done in this study and/or may require more open canopies than provided here. In addition, to preserve the biotic distinctness of the groundcover vegetation in a habitat type like these open oak woodlands, it would ultimately be necessary to include the more range-restricted endemics in such plantings. Assuming most or all species could survive competition from *Microstegium*, such a planting scheme could help to preserve global biodiversity and local biotic resistance to invasion. However, no type of biodiversity management will likely be effective at preventing invasion by species that are vastly competitively superior to the resident species.

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VITA

EDUCATION

M.S. in Biology University of Mississippi, University, MS Advisor: J. Stephen Brewer, Ph.D.	2014 – 2016
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PUBLICATIONS AND MANUSCRIPTS

- Brewer JS, Abbott MJ, **Moyer SA** (2015) Effects of oak-hickory woodland restoration treatments on native groundcover vegetation and the invasive grass, *Microstegium vimineum*. Ecological Restoration 33: 256-265.
- Moyer SA and Brewer JS. Competitive effects of increased plant species richness and increased endemic versus native generalist species dominance on the non-native invasive grass *Microstegium vimineum* during oak woodland restoration. (*In preparation*)

GRANTS AND AWARDS

Graduate Student Travel Grant to ESA Fort Lauderdale \$735	2016
Sigma Xi GIAR \$370	2015

EXPERIENCE

TEACHING

Teaching Assistant, University of Mississippi <ul style="list-style-type: none">BISC 105 Ecology and Environment Laboratory	Spring 2015, 2016
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- BISC 322 General Ecology Laboratory Spring 2015, 2016
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RESEARCH

Research Assistant, Brewer Lab, University of Mississippi Fall 2014 – Fall 2016

- Assisted with surveys of vegetation groundcover at oak woodland restoration sites
- Assisted in collection of forestry metrics (*e.g.* diameter-at-breast-height) at oak woodland restoration sites
- General field experiment set-up and maintenance

Directed Independent Study, Miller Lab, Florida State University Summer 2012

- Completed undergraduate research project examining the landscape ecology of barrier island plant communities, St. George Island, FL
- Established botanical transects, measured soil pH and gravimetric soil moisture

PRESENTATIONS

Moyer SA and JS Brewer. Competitive effects of increased plant species richness on a non-native invasive grass during oak woodland restoration (*oral presentation*). Ecological Society of America (ESA) 2016. Fort Lauderdale, FL.

Moyer SA and JS Brewer. Competitive effects of increased plant species diversity and increased endemic versus native generalist species dominance on an invasive species during oak-hickory woodland restoration (*poster*). Society of Ecological Restoration (SER): Southeastern chapter 2015. Knoxville, TN.